Decision-Making: Are Plants More Rational than Animals?

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Abstract: A new study presents a novel experimental design and allows a test of risk sensitivity in plants. Faced with a choice between constant and variable resource supply, they make a rational decision for the option that maximizes fitness, a fact rarely observed in animals.

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Decision making: Are plants more rational than animals?

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A novel experimental design allows a test of risk sensitivity in plants. Faced with a choice between constant and variable resource supply they make a rational decision for the option which maximizes fitness, a fact rarely observed in animals.

Organisms are confronted with choices when they forage. A particularly interesting situation occurs when the same amount of resource can be obtained from either a constant or a variable source. Should an individual be risk averse and choose a constant yet modest option or should it be risk prone and choose a variable yet more promising option? The answer will depend on the biological context. According to Risk Sensitivity Theory (RST), the rational decision would be the one that maximizes fitness [1]. To do so, the individual should behave according to the fitness function of the relevant resource. If this function is accelerating (convex) at the level of resources obtained per unit time and effort, the total utility or fitness gain is larger if the variable option is chosen and the individual should show risk-prone behavior (Fig. 1). If the function is decelerating (concave), which is more likely at higher resource levels, the individual should choose a risk averse behavior [1]. A new study by Dener *et al.* [2] demonstrates that brainless pea plants are able to perform such decisions… The authors grew plants with two roots and offered them the choice to forage in pots with constant or variable nutrient concentrations.

The authors first grew plants at different constant nutrient concentrations, ranging from 0–300 mg/L fertilizer. They found that both seed number and total seed mass had

concave relationship throughout the range. In addition, the mass of the average seed increased sigmoidally in response to nutrient availability, with an inflexion point at 10–20 mg/L. According to RST, individuals should be risk prone below and risk averse above this inflexion point. In a second setup, plants were offered the choice of a pot with constant or variable nutrient concentrations. The total amount of nutrients the two pots received over the 12-week duration of the experiment was the same within a treatment, but varied across treatments with the total amount of resources being either above or below the inflexion point. The decision made by each individual plant for one of the two pots (options) was inferred from the amount of roots found at the end of the experiment in constant and variable pots (Fig. 1B). When more roots had been grown into the variable pot this indicated risk-prone behavior. Interestingly, this was indeed the case for the treatments with total amount below the inflexion point. In the treatments above this total amount, plants grew more roots in the constant than in the variable pot, thus the results exactly demonstrated the behavior predicted by RST.

The new study [2] is the first test of RST in plants instead of animals. Perhaps more remarkably, it appears to support the theory better than previous tests done with animals. It seems that large animals such as birds or humans often do not make rational decisions in terms of RST [3]. For example, human behavior is not purely economic but rather influenced by other factors such as the subjective assessment of consequences of constant versus variable gains or losses [4]. A common problem with human experiments is that it is difficult (or even impossible) to create monetary rewards in games to fitness. That is why with humans we can only make conclusions about economic rationality but not whether these decisions have fitness consequences. This link seems to be much clearer in the plant experiment: rational root allocation has direct fitness consequences. Empirical Prospect Theory [5] describes humans as risk averse regarding gains and risk prone regarding losses. However, such behavior is only rational if the individual is at the inflexion point, where the function relating economic utility to resource level turns from convex to concave [4].

Obviously no broad generalizations can be made based on this single study but if and to the extent that the existing studies represent a general pattern—should we expect plants to be more rational regarding risk sensitivity than animals? Obviously, plants differ from animals in fundamental ways. They are stuck in place and take up their resources over large external surfaces below and above the soil. Plants forage by growth plasticity, extending shoots and leaves into well illuminated patches and roots into nutrient-rich patches. Their modular structure allows them to integrate local environmental responses of shoots and roots to coordinated behavior at the level of the whole individual [6], similar to collective behavior in bacteria [7]. However, information processing is generally slow and decision-making not centralized. The plant data suggest that sophisticated cognitive abilities are not required for decision making. Plants may therefore be ideally suited to test null models in which simple mechanism may account for complex behavioral outcomes.

Testing RST using animal models involves several difficulties [3]. Experiments with birds start by training the subjects to recognize e.g. different color cues for constant and variable resource options (Fig. 1A). In a second step, individuals are tested for their choice of either risk-averse or risk-prone options. With animals, it is difficult to make independent replicate trials, standardize the biological context (e.g. resource state of the individual), measure fitness, exclude unrelated factors and to assess the cognitive mechanisms underlying the observed behavior. It is therefore perhaps not surprising that studies with animal models could thus far could not support RST to the same extent as the new work with plants did.

Despite the match between the results and RST, it is yet unclear what are the physiological controls underlying plants' ability to make such decisions. Whole-plant economy implies that individual plants should increase root allocation when nutrients are scarce [8], but parts of an individual plant show the opposite behavior. That is, roots that grow in nutrient-rich patches receive higher biomass allocation and branch more frequently than roots of the same individual in nutrient-poor patches [9]. Thus, at low nutrient levels, the

variable option may attract higher allocation but at high nutrient levels it may attract lower allocation than the constant option. This would be sufficient to produce the observed response. Could such an allocation rule vary between genotypes and thus be selected for? This has not been tested yet and deserves further attention. However, differences between Mediterranean annuals regarding architectural plasticity in response to environmental cues versus more fixed bet-hedging strategies [10] suggest that it should at least be possible. A problem that may affect animals and humans more than plants is that a seeming risk-averse behavior may be evolutionarily more stable than risk-prone behavior. In plants, the individual is less clearly defined and, in fact, is constructed as a population of repeated modular units [6], which are networked like individuals in colony-forming organisms such as social insects or quorum-sensing bacteria, the behavior of which interestingly more commonly conforms to RST [3].

The study of Dener *et al.* [2] demonstrates that theories on decision making and optimal behavior developed for animals and humans can be applied to plants, which may sometimes even serve as more suitable models. The split-root approach offers excellent experimental opportunities for such research. For example, it would be easy to change the kind of variability in the resource by using different temporal regimes to test how fast plants can respond by growth plasticity. Another recent study used split-root systems to test market theory: a single plant connected to a more beneficial mycorrhizal partner in one root compartment and to a less beneficial one in the other could force the latter one to cooperate [11]. Without the choice, the plant had to provide more carbon to the less beneficial partner to receive the same amount of phosphorus from it.

Further examples using plants as models include habitat selection [12], foraging strategies [13], division of labor [14], cooperation [15] and communication [16]. In all these cases an advantage of plant models is that they allow testing of general hypotheses in the absence of a central nervous system. As an increasing number of recent studies show [17], it

turns out that complex centralized cerebral processes are not necessary for rational decision making and that simpler physiological mechanisms facilitating networks between different organs on the same individual [18, 19] or between individuals [20] can produce 'social intelligence' with complex adaptive behavioral outcomes. Despite the more than 1.5 billion years of independent evolution, plants and animals show similarities in major behavioral patterns that are based on totally different mechanisms. The similarities may even be larger if the microscopic network of neurons in the brain is compared with the macroscopic network of modules or individuals in plants and other 'simple' organisms.

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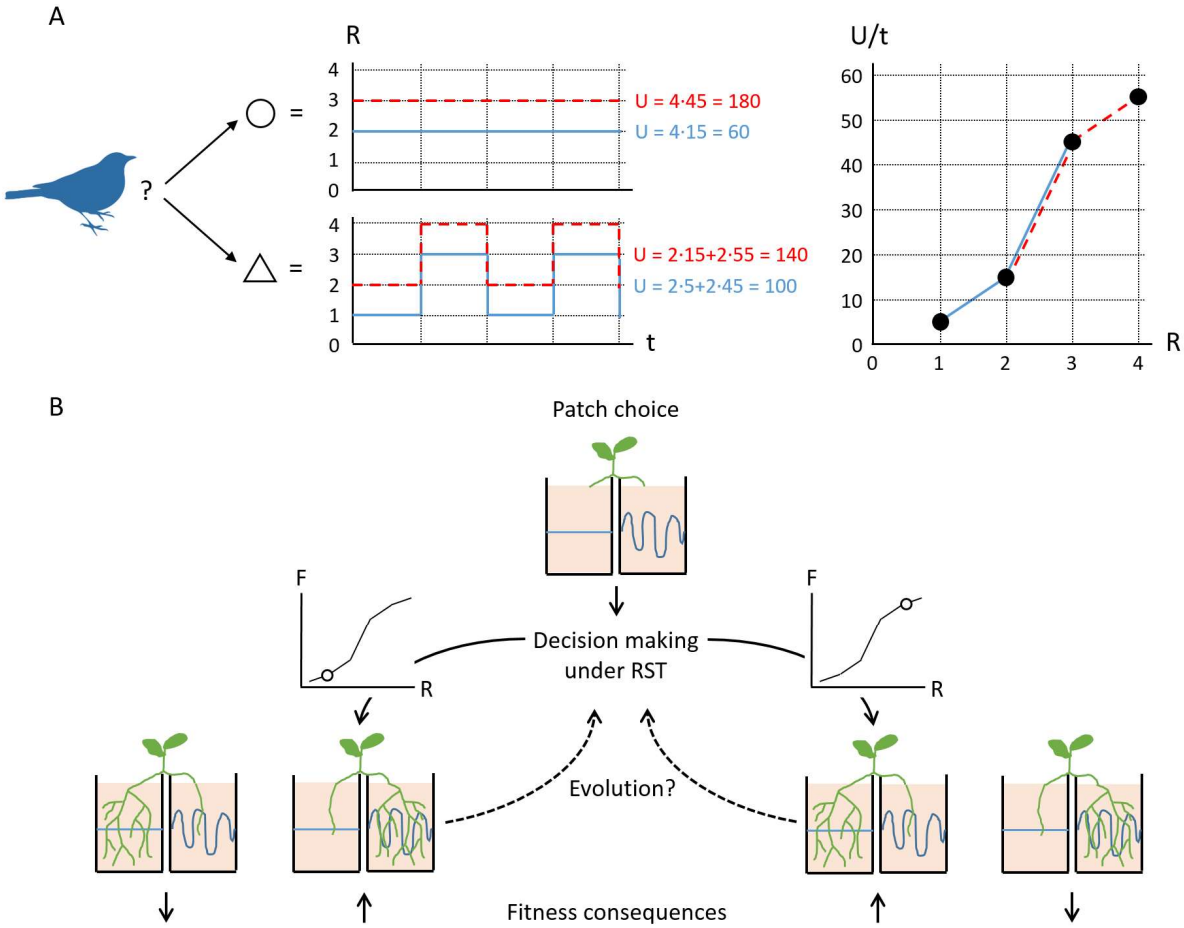
Figure 1. Predictions of Risk Sensitivity Theory (RST) in animals and plants. (A) A bird trained to distinguish between a constant (circle) and a variable (triangle) resource [3] is expected to choose the latter if the function relating resource uptake (R, e.g. number of seeds eaten) to utility per time (U/t, arbitrary units) is convex (blue, solid line) as the same amount of total resource uptake leads to a greater total utility (U). When the function is concave (red, dashed line), total utility is greater for constant than variable resource availability. (B) A plant with a split-root system [2] preferentially allocates biomass to roots in a pot with variable resource concentrations when the average resource concentration is low and fitness returns (F) are accelerating with increasing resource level (circle in the left plot relating F to R). In contrast, the plant shows a risk-averse behavior when average resource concentration is high and fitness gains are decelerating with increasing resource level (right side). This has been shown in [2] for pea plants. It is not known, however, whether the optimal decision demonstrated by pea plants is adaptive.


A
R
U/t
U = 4·45 = 180
U = 4·15 = 60
U = 2·15+2·55 = 140
U = 2·5+2·45 = 100
t
R
B
Patch choice
F
R
Decision making
under RST
F
R
Evolution?
Fitness consequences